

A Review of the Carolinian Province *Americoliva nivosa* Complex (Gastropoda: Olividae) with the Description of a New Subspecies

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ABSTRACT The common eastern North America and Gulf of Mexico olive shell, *Americoliva nivosa* (Marrat, 1871), is now known to comprise five separate subspecies that are distributed from Cape Hatteras to the Florida Keys, throughout the Gulf of Mexico to Isla Mujeres, and into the open Atlantic as far as Bermuda. The subspecies, which have disjunct distributions, include: *Americoliva nivosa clenchi* new subspecies (described here) which ranges from Cape Hatteras to Fort Pierce, Florida; *Americoliva nivosa bollingi* (Clench, 1934), which ranges from Palm Beach County, Florida south to the Florida Keys and Dry Tortugas; *Americoliva nivosa choctaw* Petuch and Myers, 2014, which ranges from Apalachicola to Pensacola along the Florida Panhandle of the northern Gulf of Mexico; *Americoliva nivosa maya* (Petuch and Sargent, 1986), which ranges from the Bay of Campeche to Isla Mujeres along the Yucatan Peninsula of Mexico; and *Americoliva nivosa nivosa* (Marrat, 1871), which is endemic to the island of Bermuda. All five of these distinct subspecies may have evolved from a common ancestor, the mid-Pleistocene (Ionian Age) *Americoliva nivosa murielae* (Olsson, 1967) from the Bermont Formation of southern Florida. A type locality is also designated for Marrat's non-localized *Americoliva nivosa*.

KEY WORDS Gastropoda, Olividae, *Americoliva*, *Americoliva nivosa*, *Americoliva nivosa clenchi*, North Carolina, Florida, Florida Keys, Gulf of Mexico, Yucatan, Bermuda, Bermont Formation

INTRODUCTION

The Carolinian Molluscan Province is now known to house a large number of distinct species and species complexes in the olivid genus *Americoliva* Petuch, 2013, with at least 12 recognizable taxa occurring within the province's five subprovincial subdivisions (Petuch, 2013; Petuch and Myers, 2014a). One of these, a Carolinian cluster of subspecies of the Caribbean Province *A. nivosa* (Marrat, 1871) (Bermudan Subprovince) was found to comprise five readily-separable taxa, with four being confined to Carolinian subprovinces and one to the Bermudan Subprovince of the Caribbean Province. The poorly-known

nominate subspecies, *A. nivosa nivosa*, had no recorded type locality and was essentially a *nomen dubium*. Based upon specimens from shallow water in Bermuda, this large, pink-colored olive was given the name "*Oliva (Strephona) bifasciata jenseni*" by Petuch and Sargent in 1986. The confusion over the status of Marrat's taxon was recently clarified by the refiguring of the type specimen of *A. nivosa* in color (in the "Mollusca Types of Great Britain" website). This has shown that the pale-colored Bermudan shells used by Petuch and Sargent to describe their subspecies *jenseni* were identical to the type lot of the true *A. nivosa*. A third member of this subspecies complex, *A. nivosa bollingi*, was described by Clench (1934) as a

southeastern Floridian subspecies of the widespread Caribbean Province *A. reticularis* (Lamarck, 1811). A fourth Carolinian member of the *A. nivosa* Complex, *A. maya*, was described from the Yucatan Peninsula (Yucatanian Subprovince) by Petuch and Sargent (1986) and is here referred to as *A. nivosa maya*. More recently, a new subspecies was also discovered and named "*A. bollingi choctaw*" (see Petuch and Myers, 2014b), adding a fourth taxon to the complex (considered here as *A. nivosa choctaw*). Since *A. nivosa* is the oldest name for the group, the cluster of subspecific taxa is referred to here as the "*Americoliva nivosa* Complex". Once the geographical distributions of *A. nivosa* and its subspecies were better known and defined, we found that the large, darkly-colored "*A. bollingi*" from North and South Carolina, Georgia, and eastern Florida represented yet another unnamed subspecies. This distinctive taxon is described in the following sections and its discovery demonstrates that the *A. nivosa* Complex actually encompasses five distinct subspecies.

Much of the confusion surrounding the Carolinian *Americoliva* species is the result of the synonymies produced by Abbott (1974: 232). He considered *A. nivosa* to be merely a form of the widespread Caribbean Province *A. reticularis* (Lamarck, 1811), and also synonymized many other valid taxa under that single species (many were later resurrected in Petuch and Sargent, 1986). The true *A. reticularis* is now known to extend from the eastern Yucatan Peninsula, Cuba, the Bahamas, across the Antillean Arc and the Lesser Antilles, to Trinidad and northern Venezuela. This wide-ranging shell differs from the members of the *A. nivosa* Complex in having a much more inflated shell with more rounded sides and in having a much coarser and more diffuse color pattern (see Figure 3E, F). The taxonomic consolidation

that was initiated by Abbott was further compounded by Tursch and Greifeneder (2001), who considered most of the Carolinian and Caribbean *Americoliva* species to belong to a single taxon, *A. fulgurator* (Röding, 1798). That characteristic southern Caribbean olive, however, is now known to be endemic only to Aruba and northern Venezuela (Petuch, 2013: 133-135) and does not range across the entire western Atlantic. This excessive "lumping" of all of these "tent-patterned" olives has only led to the obfuscation of the evolutionary patterns that have occurred within the post-Pleistocene western Atlantic. The biogeographical and distributional patterns seen in the malacofaunas of the western Atlantic still offer the best insights into biodiversity, especially in taxa with non-dispersing direct larval development or short-lived veliger stages like those seen in many of the *Americoliva* species. Using this biogeographical approach, we here propose a new taxonomic framework for this conspicuous and important group of olive shells.

SYSTEMATICS

The members of the *Americoliva nivosa* subspecies complex are arranged here biogeographically by their resident subprovinces. The holotype of the new subspecies is deposited in the type collection of the Department of Malacology, Los Angeles County Museum of Natural History, Los Angeles, California and bears a LACM catalog number.

Class: Gastropoda
 Subclass: Orthogastropoda
 Superorder: Caenogastropoda
 Order: Sorbeoconcha
 Infraorder: Neogastropoda
 Superfamily: Volutoidea
 Family: Olividae
 Subfamily: Olivinae

Genus: *Americoliva* Petuch, 2013

The *Americoliva nivosa* Complex

Diagnosis. Shells of average size for the family Olividae and the genus *Americoliva*, distinctly cylindrical in shape, with straight sides and only slightly-rounded shoulders; spires proportionally low, subpyramidal or flattened; color patterns composed of variable amounts of triangular reticulations (“tenting pattern”) and amorphous zig-zags; mid-body of body whorl with two broad bands of larger and more darkly-colored zig-zag flammules, one anterior of the mid-body line and one posterior of the mid-body line; shell base colors usually in shades of canary yellow, pale yellow-tan, pale bluish-white, or pale pinkish-white; apertures uniformly narrow; columella ornamented with numerous strong teeth, with many having distinct bifurcations.

Discussion.

This complex of subspecies is almost completely confined to the Carolinian Province, with only one known extra-provincial outlier. Four of the subprovinces of the Carolinian Province, the Georgian, Floridian, Suwannean, and Yucatanian, each contain a single *A. nivosa* subspecies, with no known members of this complex being found along the Texan Subprovince of the Texan and northeastern Mexican coastlines (the individual subspecies are listed and discussed in the following sections). The single extra-provincial subspecies, *A. nivosa nivosa*, is endemic to the isolated North Atlantic island of Bermuda and is a biogeographical index taxon for the Bermudan Subprovince of the Caribbean Molluscan Province. Its presence on Bermuda demonstrates that the complex is present in two separate faunal provinces. The distributions of the *A. nivosa* subspecies and the extents of the

subprovinces of the Carolinian Province are shown here on Figure 1.

Of the Caribbean Province congeners of the Carolinian *Americoliva nivosa* Complex, *A. bifasciata* (Küster, 1878) is the most closely-related sister species. As seen here in Figure 3 C and D, this wide-ranging Caribbean olive differs from members of the *A. nivosa* complex in being a much squatter, more inflated and rotund shell, with rounded sides and a more rounded, less cylindrical shell profile. The Caribbean *A. bifasciata* also has a proportionally higher spire than its Carolinian sister species and subspecies to the north, which is structurally more similar to *A. sayana* (Figure 3A, B) than it is to the flatter-spined *A. nivosa* (Figure 2 A, B). The Caribbean and Carolinian sister species both exhibit two central bands of dark brown zig-zags, but that character occurs in most of the other Atlantic *Americoliva* taxa as well and simply represents a shared ancestral plesiomorphic state (see Petuch and Sargent, 1986 and Petuch, 2013 for illustrations of the other western Atlantic *Americoliva* species).

The *A. nivosa* Complex appears to have evolved within the Okeechobean Paleosea of southern Florida and later spread westward into the Gulf of Mexico and northward to the Carolinas and Bermuda. The oldest-known obvious member of the complex is *Americoliva nivosa murielae* (Olsson, 1967) (originally described as a full species; Figure 3G, H) from the Belle Glade Member of the Bermont Formation (Ionian Age of the mid-Pleistocene), which indicates that the complex is approximately 1 million years old.

1. Georgian Subprovince, Carolinian Province

Americoliva nivosa clenchi Petuch &
Berschauer, new subspecies
(Figure 2C, D)

Description. Named as a subspecies of the Bermudan endemic *Americoliva nivosa nivosa*; shell large for genus and species complex, elongated, distinctly cylindrical, with straight sides; shoulder slightly rounded; spire proportionally-low, subpyramidal, with spire whorls covered by thick callus; filament channel proportionally large and deep, bordered by thin, blade-like raised edge; aperture uniformly narrow, flaring slightly at anterior end; columellar area ornamented with 20-22 large, thin teeth, with anterior teeth occurring in bifurcated pairs; shell base color bright yellow-tan overlaid with dense network of darker tan and light brown triangular reticulations and nebulous flammules; mid-body bounded by 2 bands of darker brown triangular flammules arranged in zig-zag pattern; spire callus dark tan; interior of aperture pale violet or purple-tan; anterior end of columellar fasciole purple-tan in color; edge of filament channel along shoulder canary yellow in color, marked with scattered pale blue patches and numerous prominent dark brown, elongated hairlines.

Material Examined. HOLOTYPE - length 57 mm, width 24 mm, from Onslow Bay, North Carolina, LACM 3753. OTHER MATERIAL EXAMINED - Paratype 1: length 52 mm, width 21 mm, from off Fort Pierce, St. Lucie County, Florida, in the research collection of the senior author; Paratype 2: length 33 mm, width 16 mm, from off Jacksonville, Duval County, Florida, in the research collection of Pierre Recourt.

Type Locality. Trawled by scallop boats from 25 m depth on an *Argopecten gibbus*

carolinensis scallop bed, in Onslow Bay, south of Beaufort, Carteret County, North Carolina.

Distribution. This northern subspecies ranges from Cape Hatteras, North Carolina to off Fort Pierce, St. Lucie County, Florida and is confined to the Georgian Subprovince of the Carolinian Province.

Etymology. Named for the late Dr. William J. Clench of Harvard University, for many decades the preeminent authority on the systematics of the tropical western Atlantic mollusks and the first person to recognize *Americoliva nivosa bollingi* as a valid subspecies.

Discussion. Of the known geographical subspecies of *Americoliva nivosa*, *A. nivosa clenchi* is the largest, most elongated, and most darkly-colored. The large size and cylindrical shape of this northern subspecies has led many researchers and collectors to consider the shell to be only an offshore, deeper water variant of the common and widespread *A. sayana* (Ravenel, 1834) (Figure 3A, B). The new subspecies differs from its sympatric congener in being a wider, thicker, and proportionally more cylindrical shell, in consistently having a lower spire, and in being a more darkly-colored shell with a coarser network of triangular reticulations. The new subspecies, *A. nivosa clenchi*, is also similar to the southern Florida and Florida Keys *A. nivosa bollingi* in having a distinctly cylindrical shape, but differs in being consistently larger and more elongated and in having a darker color pattern composed of a dark yellow base color and dark tan reticulations. Both *Americoliva sayana* and *A. nivosa clenchi* occur together in the deeper water scallop beds found offshore of the Carolinas, Georgia, and eastern Florida.

2. Floridian Subprovince, Carolinian Province

Americoliva nivosa bollingi (Clench, 1934)
(Figure 2 A, B)

Range. From Jupiter, Palm Beach County, Florida south to Key West and the Dry Tortugas, Florida Keys, usually found in carbonate sand near living coral reefs. Specimens of *A. nivosa bollingi* were found together with *A. sayana* on the sand flats off Peanut Island, Lake Worth, Palm Beach County, demonstrating that the two congeners are sympatric.

Discussion. This distinctive subspecies originally was described as a subspecies of *A. reticularis* and was thought to represent a southern Florida population of that wide-ranging Caribbean species. It is now known that *A. reticularis* (Figure 3E, F) is morphologically quite different from the Carolinian Province *A. nivosa bollingi* and represents a separate species lineage within the genus *Americoliva*. The Caribbean-restricted *A. reticularis* is a very inflated, almost ovate, shell with conspicuously rounded sides and with a higher, more protracted spire. The Caribbean congener also has a much more diffuse color pattern, composed of widely-separated zig-zag flammules and lacks the two mid-body bands that are so obvious on the members of the *A. nivosa* Complex. Although common in the Bahamas, *A. reticularis* has never been collected in Florida, in the Florida Keys, or anywhere else within the Carolinian Province.

3. Suwannean Subprovince, Carolinian Province

Americoliva nivosa choctaw
Petuch and Myers, 2014 (Figure 2E, F)

Range. Confined to the northern end of the Suwannean Subprovince, from the “Panhandle” of northwestern Florida and the northeastern Gulf of Mexico, from St. George Sound and Apalachicola Bay, Franklin County in the east to Pensacola Bay, Escambia County in the west.

Discussion. This isolated subspecies is the smallest member of the complex, averaging only 43 mm in length. Besides the consistent difference in size, *A. nivosa choctaw* also differs from the other sibling subspecies in having a noticeably squatter and more compressed shell with more rounded sides, in having a slightly higher spire, and in having a much finer reticulated triangle pattern on the body whorl. This is also the palest-colored member of the subspecies complex, with many specimens having only a pale tan or yellow-tan reticulated pattern.

4. Yucatanean Subprovince, Carolinian Province

Americoliva nivosa maya
(Petuch and Sargent, 1986) (Figure 2G, H)

Range. Confined to the Yucatan Peninsula of Mexico, from Isla Contoy, Quintana Roo in the east to Campeche in the west and encompassing the entire offshore Campeche Bank.

Discussion. Although originally described as a full species, distinct from other members in its genus, we now consider *maya* to be a subspecies of *A. nivosa*. This conclusion, corroborated by observations from Pierre Recourt, was reached because of the obvious similarities of *maya* with other members of the *A. nivosa* Complex. These include the cylindrical body shape, the proportionally low spire, and the presence of two dark brown bands of brown zig-zags around the mid-body. Most *A. nivosa maya* exhibit a bright canary yellow base

color, have a yellow color within the interior of the aperture, and have a yellow callus on the spire whorls. A pale yellow-colored population of the Mayan Olive has also been collected in shallow water near Isla Mujeres.

5. Bermudan Subprovince, Caribbean Province

Americoliva nivosa nivosa
(Marrat, 1871) (Figure 2I, J)

Range. Confined to the island of Bermuda.

Discussion. This is the only member of this close-knit subspecies complex that is found outside of the boundaries of the Carolinian Province, being confined to, and being a biogeographic index taxon for, the Bermudan Subprovince of the Caribbean Province. During the mid-Pleistocene, with warmer water temperatures and a faster-flowing Gulf Stream, the short-lived planktonic larvae of *A. nivosa murielae* made their way to the remote seamount of Bermuda. With no other olivid competitors and in complete genetic isolation, the Bermudan population of the Ionian-aged *A. nivosa murielae* evolved into the living *A. nivosa nivosa*. This member of the subspecies complex is the most morphologically-distinct of the five known taxa, having a pale pink or pinkish-white base color overlaid with a pale pinkish-tan reticulated pattern. The Bermudan subspecies also closely resembles the ancestral *A. nivosa murielae* (Figure 3G, H) in having the same cylindrical shape, flattened spire, and shell size.

Marrat (1871) gave no type locality for his “*Oliva*” *nivosa* (see Mollusca Types of Great Britain website) and the species name has been applied erroneously to many other Caribbean *Americoliva* species, most often variants of *A. bifasciata* and *A. figura*. An examination of

Marrat’s syntypes has shown that the taxon is identical to the holotype of “*Oliva (Strephona)*” *bifasciata jenseni* Petuch and Sargent, 1986 (deposited in the National Museum of Natural History, Smithsonian Institution, catalog number USNM 841453; see Petuch and Sargent, 1986, plate 21, figs. 16 and 17). Since Marrat’s *nivosa* is now known to be endemic to the island of Bermuda, we here designate its type locality as “2 m depth in sand, off Blue Horizons Beach, Paget County, Bermuda”.

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Figure 1. Map showing the distributions of the five subspecies in the *Americoliva nivosa* Complex.

A= *Americoliva nivosa clenchi* Petuch and Berschauer, new subspecies; **B=** *Americoliva nivosa bollingi* (Clench, 1934);

C= *Americoliva nivosa choctaw* Petuch and Myers, 2014; **D=** *Americoliva nivosa maya* (Petuch and Sargent, 1986); **E=** *Americoliva nivosa nivosa* (Marrat, 1871).

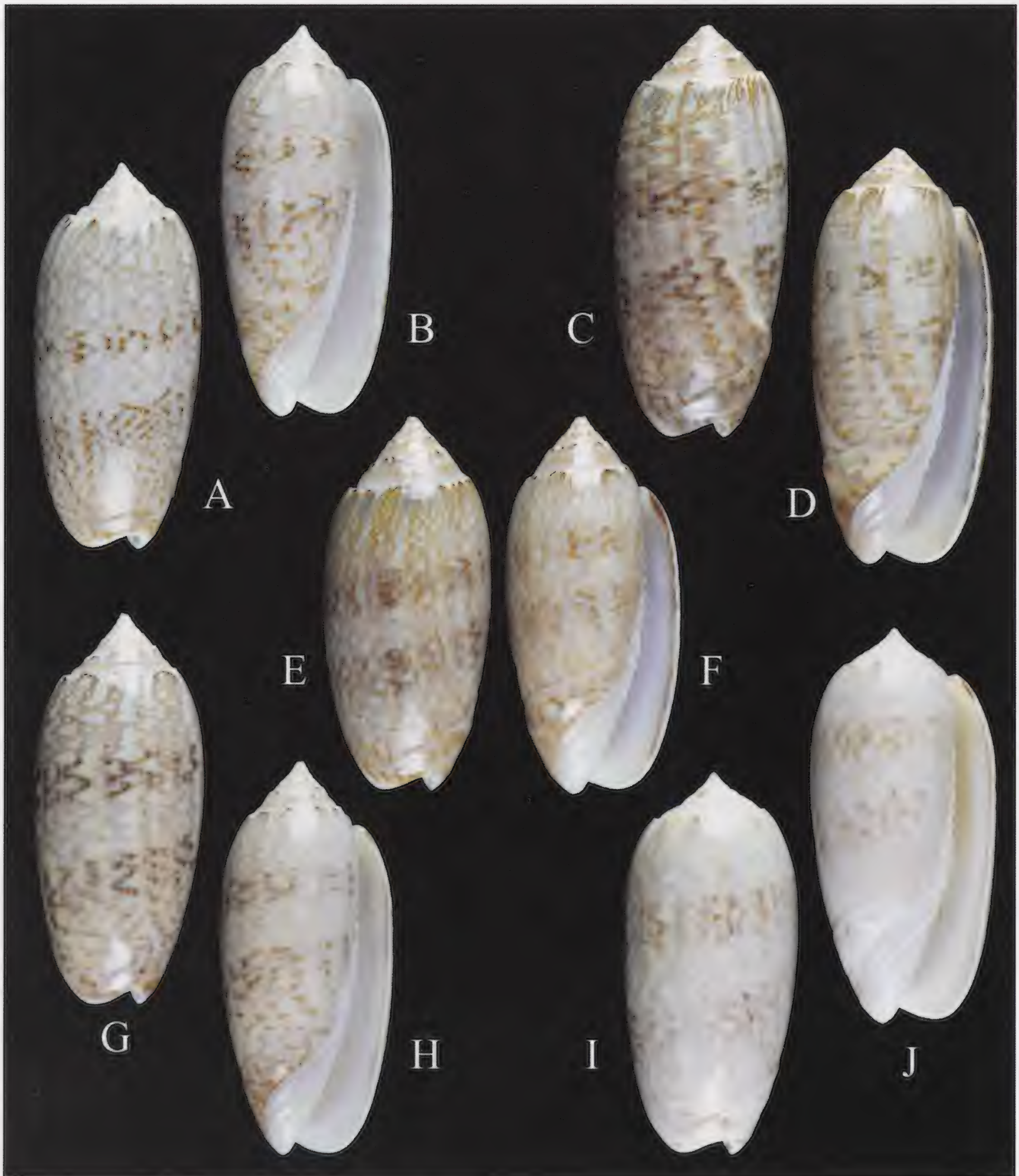


Figure 2. Subspecies of *Americoliva nivos* (Marrat, 1871). A, B= *Americoliva nivos bollingi* (Clench, 1934), length 52 mm, from 3 m depth on carbonate sand, off Boca Raton, Palm Beach County, Florida; C, D= *Americoliva nivos clenchi* Petuch and Berschauer, new subspecies, holotype LACM 3753, length 57 mm, trawled from 25 m depth in an *Argopecten gibbus carolinensis* scallop bed, in Onslow Bay south of Beaufort, Carteret County, North Carolina; E, F= *Americoliva nivos choctaw* Petuch and Myers, 2014, length 40 mm, in sand at low tide, St. Andrew Sound, Panama City, Bay County, Florida; G, H= *Americoliva nivos maya* (Petuch and Sargent, 1986), length 50 mm, trawled from 30 m depth off Isla Contoy, Quintana Roo, Mexico; I, J= *Americoliva nivos nivos* (Marrat, 1871), length 48 mm, from 2 m depth in sand off Blue Horizons Beach, Paget Parish, Bermuda; *A. bifasciata jenseni* (Petuch and Sargent, 1986) is a junior synonym).



Figure 3. Living and fossil *Americoliva* species from the Carolinian and Caribbean Provinces. A, B= *Americoliva sayana* (Ravenel, 1834), length 64 mm, 2 m depth in sand, off Jupiter Beach, Jupiter, Palm Beach County, Florida; C, D= *Americoliva bifasciata* (Küster, 1878), length 50 mm, 2 m depth in sand off the southern coast of Ile Gonave, Haiti; E, F= *Americoliva reticularis* (Lamarck, 1811), length 45 mm, low tide in sand, Nixes Harbour, South Bimini Island, Bahamas; G, H= *Americoliva nivosa murielae* (Olsson, 1967), length 49 mm, from the Belle Glade Member of the Bermont Formation, Ionian Age, Pleistocene. Collected in spoil piles from the dredging of the North New River Canal, 5 km south of South Bay, Palm Beach County, Florida.